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Disentangling effects of structural deadwood characteristics on fungal and bacterial diversity and assembly processes

Henrik Oechler[a,*], Franz-Sebastian Krah[a,b], Jasper Schreiber[c,d], Petr Baldrian[e], Vendula Brabcová[e], Harald Kellner[f], Friederike Roy[f], Claus Bässler[a,g]

[a] Fungal Ecology, Faculty of Biology, Chemistry & Earth Sciences, University of Bayreuth, Bayreuth, Germany
[b] Global Change Research Institute, Czech Academy of Sciences, Brno, Czech Republic
[c] Institute of Ecology, Evolution and Diversity, Goethe University Frankfurt, Frankfurt Main, Germany
[d] Department of Landscape Planning and Nature Conservation, Hochschule Geisenheim, Geisenheim, Germany
[e] Laboratory of Environmental Microbiology, Institute of Microbiology, Czech Academy of Sciences, Prague, Czech Republic
[f] International Institute Zittau, Department of Bio- and Environmental Sciences, TU Dresden, Zittau, Germany
[g] Bavarian Forest National Park, Grafenau, Germany

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ABSTRACT

Forest ecosystems face increasing pressure from the growing demand for wood and global change, yet the ecological consequences of management decisions remain incompletely understood. Deadwood is a key component in forest ecosystems, supporting biodiversity and biogeochemical cycles. However, the role of deadwood characteristics, the abiotic environment, and its interactions for fungal and bacterial diversity is not fully understood. We experimentally assessed how different combinations of key deadwood characteristics influence microbial diversity and community assembly, using both molecular (within wood) and fruit body sampling. Four types of logs (soil-contacting, non-soil-contacting, debarked, and bark-intact) were placed under open and closed canopies to manipulate strong contrasts in microclimatic conditions. We found that bark retention had a stronger effect on microbial alpha and beta diversity than soil contact or canopy cover. Debarking increased fungal and bacterial molecular diversity (e.g., fungal richness increased by ~20 OTUs per log on average) while decreasing phylogenetic diversity more than expected, indicating abiotic selection of narrower but species-rich lineages. Fungal fruit body diversity showed a contrasting pattern with an increased diversity under open canopies, barked trees, and soil contact, suggesting a combination of enhanced fruiting cues and benign growing conditions. Observed patterns were largely explained by differences in deadwood moisture conditions. To maintain microbial diversity across multiple facets, it is crucial to vary both soil contact and bark retention when enriching deadwood. Management approaches that prioritize characteristics enhancing only alpha diversity may inadvertently reduce phylogenetic diversity and, consequently, functional potential.

1. Introduction

The aim of modern forestry is multifunctional forests that fulfill both the exploitation of resources and the conservation of biodiversity (Gustafsson et al., 2012; Sing et al., 2018). However, one major trade-off within this concept is that the main goal of timber production can have negative consequences on biodiversity via a change in tree species composition towards productive tree species and the reduction of dead and senescent trees (Dieler et al., 2017; Tinya et al., 2021; Tomao et al., 2020). A further challenge today is climate change, which increases the severity and frequency of canopy disturbances and thus changes resources and the abiotic conditions for forest organisms (Baldrian et al., 2023; Patacca et al., 2023; Seidl et al., 2017). However, our understanding of the ecological consequences of these forest structural changes is limited. In particular, the link between complex deadwood types, the abiotic environment, and microbial diversity remains poorly understood. To address this challenge, we established a controlled deadwood experiment designed to separate key abiotic and biotic factors and test their impact on microbial diversity and community assembly.

Forest management and climate-induced changes in forest structure can occur across multiple scales. We focus on the stand- and object-scale,

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* Correspondence to: Universitätsstraße 30, Bayreuth 95440, Germany.
E-mail address: henrik.oechler@uni-bayreuth.de (H. Oechler).

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as these represent the levels at which management measures can be most directly implemented. On the stand-scale, the deadwood objects are exposed to variations in canopy-mediated microclimate. The canopy mitigates excessive heating effects of solar radiation, as well as cooling at night (De Frenne et al., 2019). Consequently, changes in canopy cover are among the most direct and rapid drivers of microclimatic variation, with openings strongly increasing temperature variability for deadwood (Schreiber, Pouska, et al., 2025). Thus, open canopies might create a stressful environment for sessile forest organisms (Thom et al., 2020). Indeed, it has been shown that benign microclimates under closed canopy conditions increased fungal and bacterial biomass and richness on deadwood (Brabcová et al., 2022; Tláskal et al., 2025). However, other studies reported no significant relationships between canopy cover and microbial richness, indicating context dependency in relation to the stand-scale microclimate effects (Hagge et al., 2024; Uhl et al., 2022). Overall, most studies in this context revealed that object-scale variables explained more variance of microbial diversity than stand-scale microclimate (e.g., Baber et al., 2016; Englmeier et al., 2023; Hagge et al., 2024; Krah et al., 2018; Rieker et al., 2022). Among these object-scale factors, host tree species identity has been most frequently studied and shows consistent effects on microbial diversity (Baber et al., 2016; Krah, Seibold, et al., 2018; Moll et al., 2021; Purahong et al., 2018; Rieker et al., 2022). However, other deadwood characteristics that contribute to explaining differences in microbial diversity are deadwood dimensions (Küffer et al., 2008; Mamadashvili et al., 2024; Pioli et al., 2023) and decay stage (Bässler et al., 2012; Hoppe et al., 2015; Kubartová et al., 2012), underpinning the complexity of deadwood characteristics and the related microbial diversity.

To date, the object-scale factors that have received less attention include bark retention and the degree of soil contact. These factors may also influence microbial diversity, particularly in different microclimates. First, soil contact affects deadwood moisture and provides a source of colonizing species (Jaroszewicz et al., 2021; Mäkipää et al., 2017). Differences in the amount of soil contact can result from natural processes such as windthrow, branch breakage, or uprooting, as well as from standing deadwood or large branches in intact or disturbed crowns (Priewasser et al., 2013; Ruel, 1995; Swanson et al., 2011). Second, bark presence shapes communities by providing structural and chemical defenses (Franceschi et al., 2005). Additionally, different levels of bark might vary in moisture conditions and thus could affect microbial communities. Bark removal can occur through insect activity, sun exposure after canopy changes, or handling during logging operations (Kautz et al., 2023; Langer and Bußkamp, 2023; Nill et al., 2011). In summary, although some object-scale characteristics are well studied, we still lack a clear understanding of how multiple deadwood characteristics interact under varying stand-scale microclimatic conditions to

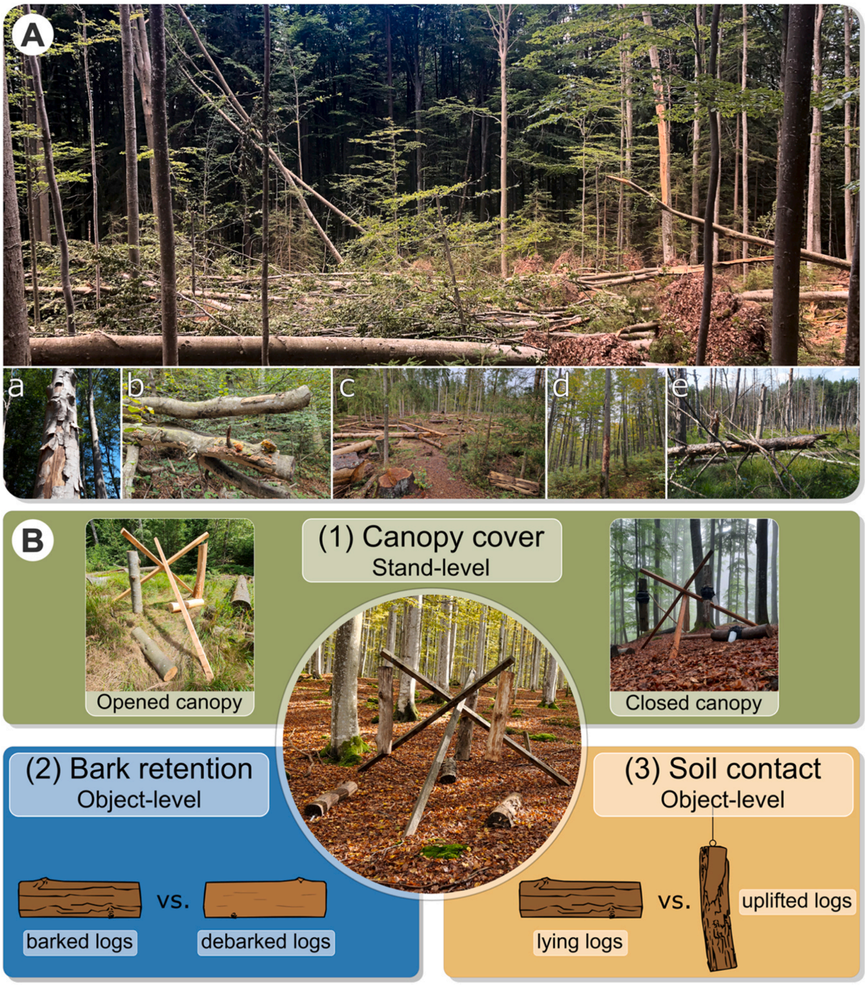

Fig. 1. (A) Natural and anthropogenic disturbances lead to different combinations of deadwood characteristics: a) Debarking and subsequent death of beech tree caused by canopy opening (Image by Christoph Hentschel, Regionalforstamt Soest-Sauerland) b) Fungal colonization of deadwood without soil contact. c) Managed disturbance area with manually debarked trunks for pest control d) Natural debarking of standing beech under an undisturbed canopy e) Branches of a broken crown limiting soil contact ("Deadwood in Müritz National Park, Germany" by Harke licensed under CC-BY-SA). (B) Experimental design simulating characteristics: With our experimental setup, we investigate the influences of (1) the site-specific level of canopy cover, (2) the object-related amount of bark retention, and (3) the degree of soil contact on microbial diversity.

shape microbial diversity and community assembly.

To disentangle the effects of the object-scale factors of bark retention (barked versus debarked) and soil contact (lying versus uplifted), as well as stand-scale canopy cover (open versus closed), on microbial diversity patterns and assembly processes, we set up an experiment with orthogonal manipulation of these deadwood features (Fig. 1). We used metabarcoding to characterize fungal and bacterial communities and additionally used fruit body identification for fungi. We expect that the relative importance of object-scale factors is higher than stand-scale canopy cover in explaining microbial diversity (e.g., Krah et al., 2018; Uhl et al., 2022). We further expect that bark retention and soil contact reflect benign microclimate conditions (e.g., buffering temperature and moisture extremes) for microbial growth and thus, should increase microbial diversity in contrast to debarked and uplifted objects (Brabcová et al., 2022; Tláskal et al., 2025). Expected diversity differences might be even more pronounced under closed compared to open canopies due to stand-scale microclimate buffering effects (De Frenne et al., 2019). Benign conditions might be particularly related to increased moisture conditions of objects with bark retention and soil contact in closed canopies, and thus, moisture might contribute to explaining the positive diversity response. Finally, we ask whether the observed diversity patterns in relation to the treatments likely resulted from (i) a selective assembly process indicated by phylogenetic lineages on a dead wood object that are more similar or dissimilar than expected from a null model and (ii) whether the treatments reflecting environmental stress lead to a loss of phylogenetic lineages, indicated by phylogenetic lineages being even more similar than expected under the more stressful compared to the benign treatment. For example, if debarked objects reflect a stressful environment (physiological constraints) for microbial communities, eliminating species from the assemblage, we would expect lineages to be more similar than expected under a selective assembly process. Further, we would expect that the stressful treatment selects similar lineages across the dead wood logs, resulting in a loss of phylogenetic diversity due to the treatment.

Summarized, we thus hypothesize that: (H1) Object-scale factors (bark retention, soil contact) exert stronger effects than stand-scale canopy cover on microbial alpha and beta diversity. (H2) The positive effects of bark retention and soil contact on microbial diversity are stronger under closed-canopy stands than under open-canopy stands, reflecting interactive effects. (H3) Microbial alpha diversity increases with higher deadwood moisture content, highlighting that moisture conditions underlie the effects of bark retention and soil contact. (H4) Deadwood objects that are debarked, uplifted, or under open canopies reflect stressful environmental conditions, acting as a selective process indicated by lower phylogenetic alpha diversity than expected. (H5) Furthermore, these stressful environmental conditions select more strongly for similar phylogenetic lineages than their benign counterpart, indicated by lower phylogenetic beta diversity of the treatments representing stressful environments compared to the more benign treatments. To approach our hypothesis and broaden ecological inferences, we take advantage of the Hill framework and quantify the diversity separately with emphasis on rare, common, and dominant species (Chao et al., 2014). Finally, we informed the treatments with *in situ* measured microclimatic and chemical variables.

2. Methods

2.1. Study area

The experiment was conducted in the Bavarian Forest National Park located in southeastern Germany (48°54’ N, 13°29’ E). The National Park is mainly forested with Norway Spruce (*Picea abies* [Karst.]), European Beech (*Fagus sylvatica* [L.]), and Silver Fir (*Abies alba* [Mill.]). Our setup takes advantage of an existing larger-scale forest experiment within the management zone of the National Park (cf. Seibold et al., 2014, 2016). To minimize confounding effects, plots were selected for similar topography and surrounding vegetation. We used 30 plots (0.1 ha) across 5 blocks, with half of the plots artificially opened to simulate disturbance or logging events, while the others remained with a closed canopy cover, resulting in significant differences in shading between open and closed canopies beyond the size of the plot (Seibold et al., 2014). Open plots were established by cutting and subsequently maintained through annual mowing and removal of regrowth. In addition, smaller vegetation that could shade the experimental logs was regularly removed during plot visits. In 2021, four beech logs (100 cm length, ~25 cm diameter) were placed per plot. The chosen log dimensions fall within the range of coarse woody debris, as commonly defined by thresholds of $>$ 7–10 cm (Korboulewsky et al., 2021). At the same time, this size class ensured sufficient replication and manageable handling within the experimental design. Beech was chosen as a dominant and economically important species with relatively rapid early-stage decomposition (Schreiber, Kellner, et al., 2025), and to allow this study to serve as an extension of the existing beech log experiment already present at the sites. Half of the logs were exposed to soil contact, and the other half were vertically uplifted without soil contact. Of these, half were carefully debarked right before exposition using a bark spud, taking care not to damage the underlying wood, whereas the other half remained fully barked. Throughout the study period, the logs that were initially classified as barked retained their bark. In total, 120 individual deadwood logs were studied across eight treatment combinations, varying in canopy cover, bark retention, and soil contact (15 logs per combination). The logs were sourced from a small number of healthy, undamaged trees felled simultaneously within a single forest stand in the study area and were placed randomly on the experimental plots immediately after felling. We used freshly felled logs to standardize colonization history and deadwood characteristics, which would not have been possible with naturally decaying material.

2.2. Environmental variables

The categorical characterizations of the deadwood logs of our experiments are combinations of open versus closed canopy cover, logs with and without soil contact, and debarked versus barked logs. To better inform the treatment categories, we measured environmental variables directly on the logs (Table S1). The treatment categories might reflect variability in microclimate temperature and moisture conditions. Thus, microclimate temperature was measured, however, only on a subset of logs due to resource constraints. The subset includes logs on two plots under closed and two under open forest canopies, each pair near one another to reduce potential spatial bias. We used temperature buttons (MF 1922 L iButton; measuring accuracy: ± 0.5 °C) and recorded the temperature on the inside (middle of the logs) and outside (facing northwards) of a total of 16 logs hourly for the period 2021–2023. Furthermore, the moisture content of all 120 deadwood logs of the experiment was measured monthly with a handheld device (FM-300 Voltcraft) during the vegetation period over the span of three years. The device measures moisture content via an electrical current between metal spikes, which enables measurements below the bark layer of the log. The mean of 4 replication measurements taken along the length of the log (every 20 cm) was calculated. We limited the measurements to the months of the vegetation period (April to November) as this is the time of highest microbial activity, and weather conditions made some of the plots inaccessible in winter. Although our study focuses on early successional stages, different treatments may be representative of slight differences in the rate of decomposition at the time of sampling. In the early successional stage, pH, nitrogen, and carbon content have been demonstrated to reflect decomposition processes (Arnstadt et al., 2016). Therefore, we determined the nitrogen and carbon content of the deadwood, as well as the pH level (October 2022). The pH was measured in aqueous extracts of 3 g of dried and milled wood samples. 30 ml of distilled water was added to each sample, after which the samples were shaken for two hours at 180 rpm at 6°C.

Extracts were then filtered (Sterilflip 10 µm, Merck Millipore, USA) and centrifuged at 15,000 rpm and 10°C. C and N content were measured using 500 mg of dried milled wood on a VARIO EL III (Elementar, Langenselbold, Germany) according to the manufacturer's protocol.

2.3. *Diversity data*

The microbial molecular field sampling was performed after one year of exposure (October 2022), following standard protocols to avoid cross-contamination. Here, an 8 mm sterilized auger bit was used to drill through the center of the deadwood object at a 45-degree angle, ensuring maximum capture of the log's heterogeneity. To represent as much of the log as possible, two drillings were performed per log: the first 10 cm from the cut edge and the second in the center. Prior to drilling, the outermost bark layer was scraped off with a knife and cleaned with ethanol to remove surface organisms not present within the wood. The drilled material was collected in plastic bags, immediately cooled, and frozen on the same day at −40°C. The tools were mechanically cleaned (using a knife and toothbrush) and sterilized (with ethanol and flame) between drillings to prevent cross-contamination of samples.

After sampling, each sample was freeze-dried (Alpha 1–4 LSCplus, Christ, Germany) and homogenized into a fine powder using a swinging mill (Retsch, Haan, Germany). Sample DNA was isolated from ~ 0.2 g of each homogenized sample using the NucleoSpin® Soil kit (Macherey-Nagel, Germany) following the manufacturer's introductions. The cell lysis was performed using SL1 lysis buffer, Enhancer SX, and a FastPrep-24 device (MP Biomedicals, Santa Anna, USA). DNA quality and quantity were assessed using a NanoDrop spectrophotometer (NanoDrop 2000, Thermo Scientific, USA). To analyze the microbial communities, the ITS2 (fungal internal transcribed spacer) region of fungal DNA was amplified via PCR using gITS7 and ITS4 uniquely barcoded primers (Ihrmark et al., 2012), and the prokaryotic hypervariable V4 region of the bacterial 16S rRNA gene was amplified using 515 F and 806 R uniquely barcoded primers (Caporaso et al., 2011). Each sample was processed with three separate PCR reactions. Each PCR contained 5 µl of 5 × Q5 reaction buffer, 1.5 µl of BSA (10 mg ml^{-1}), 1 µl of each primer (0.01 mM), 0.5 µl of PCR Nucleotide Mix (10 mM each), 0.25 µl of Q5 High Fidelity DNA polymerase (2 U $µl^{-1}$, New England Biolabs, Inc.), 5 µl of 5 × Q5 HighGC Enhancer and 1 µl of template DNA (approx. 50 ng $µl^{-1}$). Cycling conditions were 30 cycles of 98 °C for 30 sec, 94 °C for 10 sec, 56 °C for 30 sec, and 72 °C for 20 sec, and a final extension at 72 °C for 2 min. The number of cycles was lowered to 25 for bacterial primers. PCR triplicate reaction products were pooled and purified (MinElute PCR Purification Kit, Quiagen), and amplicon libraries prepared with the TruSeq DNA PCR-Free Kit LP (Illumina) were sequenced in the Institute of Microbiology, Prague, on the Illumina MiSeq (2 × 250-base reads).

Data from the sequencing were analyzed using the SEED 2.1.3 pipeline (Větrovský et al., 2018). Paired-end reads were joined using fastq-join (Aronesty, 2013) and the ITS2 region was extracted using a built-in *ITS Extractor* (fungi only). Chimeric sequences were identified and removed using Usearch 11.0.667 (Edgar, 2010) and the sequences were grouped into clusters at 97 % similarity using the UPARSE algorithm within USEARCH 8.1.1861 (Edgar, 2013). The most frequent sequence in each cluster was chosen for further identification at the species level using BLASTn against the UNITE 10 (Abarenkov et al., 2024) or SILVA 138.1 database (Quast et al., 2012). Sequences with $\geq$ 97 % identity were assigned to the species level; for those with $<$ 97 % identity but $\geq$ 95 % query coverage, a genus-level identification was applied. Only sequences identified as fungal and respective bacterial were used in the analysis.

All deadwood logs were examined for fungal fruit bodies in October 2023 (fruiting peak). Fruit bodies were sampled on the entire log, divided into three sectors: two representing the cut edges and one representing the lateral log surface. Our measure for fruit body abundance, indicating fitness of a given species, is the number of occupied sectors per log. Species were identified in the field or, if necessary, in the lab with the use of a microscope.

2.4. *Statistical analysis*

All analyses were performed with R (Version 4.4.1). In the main analyses, we considered the treatment factors of canopy cover, bark retention, and soil contact as main predictors. To account for a potential confounding effect caused by succession, we considered the deadwood's chemical properties (pH level, carbon, and nitrogen content) as covariates. We additionally explored microclimate data to inform treatments. Although temperature records were only available for a subset of logs, their mean and variability correlated strongly with canopy treatment (Table S2; Fig. S1), consistent with previous findings (De Frenne et al., 2019; Schreiber, Pouska, et al., 2025). Moisture conditions, in turn, were closely linked to bark retention and soil contact (Table S3; Fig. S2). Therefore, in a second approach, we used mean moisture (which was strongly correlated with moisture variability; Fig. S4) and canopy as a proxy for microclimate temperature, and the wood chemical properties as covariates. The chemical covariates were not strongly affected by the applied treatments (Table S4; Fig. S3).

To account for sampling biases, e.g., uneven sequencing depth, we used the function *estimateD* of the iNEXT package (Hsieh et al., 2024) to diversity standardization of sample coverage via extrapolation and rarefaction. However, we repeated the analysis with rarefaction of molecular data using the functions *rarefy* and *rrrarefy* of the vegan package (Oksanen et al., 2024) to confirm the robustness of the main results (Schloss, 2024). We determined the rarefaction depth by inspecting read count distributions to balance sequencing depth and sample retention. We performed rarefaction of fungal OTUs to a standardized sequencing depth of 1000 reads per sample, resulting in the exclusion of 21 samples, whereas rarefaction of bacterial OTUs to 7000 reads per sample resulted in the exclusion of only 6 samples. Fungal fruit body counts are too low for rarefaction at this early stage of deadwood succession. Results based on rarefaction confirmed the main results based on the sample coverage approach (Tables S6, S8, S10, S12; Figs. S6, S11).

To approach H1, we determined the relative importance of treatments on the diversity of fungal OTUs, fungal fruit bodies, and bacterial OTUs by applying multiple linear mixed-effects models using the *lme* function of the nlme package (Pinheiro et al., 2024). We used Hill numbers where the importance of the abundance distribution increases with the Hill order: $q= 0$ for rare species (species richness), $q= 1$ for common species (exponential Shannon entropy), and $q= 2$ for dominant species (inverse Simpson index). We used linear mixed-effects models because weighting over q results in decimal diversity data and, thus, reflects most of the variability within the diversity data (particularly important for the fruit body data characterized by a low number of species per log on average). Before entering the model, the diversity data were $\log_{10}$-transformed. Note that negative binomial models, which are more appropriate for count-based data, yielded similar results after rounding the diversity values to integers (not shown). In addition to canopy cover, bark retention, and soil contact, we included chemical variables as covariates in the model. Co-linearity among predictors is weak ($|r|< 0.32$; Fig. S5). To account for spatial autocorrelation and the nested structure of our design, we additionally included a random effect term with plots nested within the blocks.

To address H2, we included interaction terms between canopy cover, bark retention, and soil contact. Since we tested the same predictors in two different models for study questions one and two, we applied a Bonferroni correction. For *post hoc* comparisons among the interaction groups, we used the *emmeans* and *emmip* functions of the emmeans package (Lenth, 2024).

Addressing H3, we modeled the alpha diversity measures as described above, but with canopy as a proxy for temperature and mean moisture as the main predictors to gain further insights about the underlying treatment effects.

We approached beta diversity like that of alpha diversity, by calculating coverage-based similarity indices with increased importance of the abundance distribution: standardized Jaccard similarity index (equivalent to q=0), the Horn similarity index (equivalent to q=1), and the Morisita-Horn similarity index (equivalent to q=2) between all pairwise assemblages based on the iNEXT.beta3D package (Chao et al., 2023). The resulting estimated dissimilarity matrices were used in a PERMANOVA with the function *adonis2* (Oksanen et al., 2024) with the same model structure as described above to approach H1 and H2. To better visualize the difference between community compositions, we performed a Nonmetric Multidimensional Scaling (NMDS) with the *metaMDS* and *vegdist* function (Oksanen et al., 2024).

Addressing H4 and H5, we applied a null modeling approach based on phylogenetic distances. We opted for this approach because compiling meaningful functional traits for all OTUs was not feasible. We follow the basic assumption that phylogenetically closely related OTUs share ecologically relevant traits that influence assembly processes (Darwin, 1859; Stegen and Hurlbert, 2011). However, we are aware that phylogenetic differences among species within a community must not necessarily reflect functional differences (Cadotte et al., 2019; Cadotte and Tucker, 2017; Kraft et al., 2015; but see: Krah et al., 2019). Nevertheless, applying a rigorous null model approach and testing whether the species within and among communities are phylogenetically more similar or dissimilar than expected by chance allows inferences about the basic assembly process (Webb et al., 2002). For example, significant standardized effect sizes (SES) from null modelling indicate selective assembly processes, while non-significant effect sizes would indicate other processes like stochasticity or drift (Dini-Andreote et al., 2015). Before applying the null model, we constructed phylogenetic hypotheses for fungi and bacteria using two genus-level backbone trees as reference (Parks et al., 2022; Tedersoo et al., 2018). Missing genera from our datasets were placed in the backbone at higher taxonomic levels. Within-genera relationships were resolved from consensus ITS (fungi) or 16S (bacteria) sequences. Sequences were aligned using the AlignSeq function of the DECIPHER package, which has been shown to perform well across simulated and empirical datasets (Wright, 2016). Phylogenetic trees were then inferred from the multiple sequence alignments with the Neighbor-Joining method in TreeLine, balancing speed and accuracy at short evolutionary scales (Kortmann et al., 2025). Branch lengths were assigned using the Grafen method (Grafen, 1997). All fungal OTUs were included in the phylogeny, whereas for bacteria 4002 of the total 5579 OTUs could be placed.

For alpha diversity (within communities), we calculated the null model–based standardized effect sizes (SES) of mean pairwise phylogenetic distance (MPD) using the *ses.mpd* function in the *picante* package (Kembel et al., 2010). Calculations were weighted by relative abundances, with 999 randomizations under the "taxa.labels" null model. The resulting values (hereafter "SES.phyloAlpha") indicate whether communities are more phylogenetically clustered (negative SES), overdispersed (positive SES), or not different from random ($|SES| \leq 1.96$).

For beta diversity (among communities), we used the *ses.comdist* function of the MicEco package (Russel, 2021) with the "taxa.labels" null model and 100 randomizations to calculate SES of pairwise phylogenetic turnover (hereafter "SES.phyloBeta"). Comparisons were structured as (i) within treatment categories (canopy cover, bark retention, soil contact) to test whether objects within a category follow alpha-diversity trends, and (ii) among treatment states to test whether different lineages are lost or gained between treatments.

Treatment and environmental effects on SES.phyloAlpha were modeled using linear mixed-effects models using the *lme* function (Pinheiro et al., 2024), and effects on SES.phyloBeta using the *lmer* function (Bates et al., 2015) with the same model structure as described above (Tables S13, S14). To account for the non-independence of pairwise comparisons, we included random effects on both samples ((1|sample1) + (1|sample2)).

To test for specific differences among treatment states, we conducted *post hoc* pairwise contrasts on the fitted beta-diversity models using *emmeans* (Lenth, 2024). Separate models were fitted for fungi and bacteria, and contrasts were extracted for canopy cover, bark retention, and soil contact (Table S15). Due to data limitations, this approach was not applied to fruit body communities.

3. Results

Molecular sampling yielded a total of 2410 fungal OTUs (78.33 ± 54.98 OTUs per log) and 5579 bacterial OTUs (281.10 ± 225.04 OTUs per log). For fungal fruit bodies, a total of 871 fruit bodies from 31 species (mean of 5.90 ± 2.53 fruit bodies per log) were recorded.

3.1. *Relative importance (H1)*

Debarking was the strongest driver of microbial alpha diversity, increasing bacterial and fungal OTU diversity but reducing fungal fruit body diversity (Table 1; Fig. 2). The strength of the effect (t-values) varied with Hill numbers: for fungal OTUs, effect sizes decreased with focus on rare (q=0) to dominant (q=2) OTUs, whereas for bacterial OTUs they increased. Bacterial richness (q=0) was not significantly affected. Canopy opening reduced fungal OTU diversity but promoted fruit body diversity, while soil contact had only a negative effect on fungal fruit bodies (Tables 1, S5).

For both groups, most of the variation in community composition was explained by bark retention, followed by soil contact and canopy cover (Table 2; Fig. 3). The strength of these effects followed the same pattern across Hill numbers, decreasing for fungal OTUs and increasing for bacterial OTUs. The sets of models better explain bacterial (R^2=0.34–0.53) than fungal community composition (R^2= 0.31–0.38).

3.2. *Interactive effects (H2)*

Fruit body diversity, considering both rare and common species, was higher under open canopies if bark was intact but unchanged under closed canopy cover if the objects were debarked (Table 1; Figs. 2, S7). Significant interactions of bark retention and soil contact were observed across Hill numbers for both fungal fruit bodies and bacteria: fruit bodies were generally less diverse in uplifted logs but more so in those that were additionally debarked. Likewise, the difference in bacterial diversity between barked and debarked logs was only present in those with soil contact (Table 1; Figs. 2, S8).

Across all models, soil contact and bark retention consistently influenced community composition (Table 2). Fungal communities of debarked and uplifted logs differed significantly from barked logs (Fig. S9), and bacterial community composition was further shaped by interactions of canopy cover with bark retention for rare OTUs, and with soil contact for dominant OTUs (Table 2; Figs. 3, S9).

3.3. *Effects of deadwood moisture (H3)*

Moisture had a significant negative influence on both fungal and bacterial OTU diversity across Hill numbers, except for bacterial richness. Diversity indices for fungal fruit bodies showed the opposite response (Table S5; Fig. 4).

The interaction of canopy cover and moisture content was only significant for fungal fruit body richness (Table S5), with higher diversity on deadwood with higher moisture content under open forest canopies (Fig. S10).

3.4. *Assembly processes (H4 and H5)*

Bark retention explained most of the variance of the standardized effect sizes of the mean pairwise phylogenetic distance within objects (SES.phyloAlpha) (Table S13). Debarking significantly decreased SES.

Table 1
Effect sizes (t-values) of the linear mixed-effects model for alpha diversity of fungal OTUs, fungal fruit bodies, and bacterial OTUs, as well as the interaction model (for the full results see Table S5).

	Fungal OTU Diversity			**Fungal fruit body Diversity**			**Bacterial OTU Diversity**		
	q= 0	q= 1	q= 2	q= 0	q= 1	q= 2	q= 0	q= 1	q= 2
(Intercept)	2.10	2.21	2.13	0.30	0.30	0.52	0.81	0.87	0.77
Canopy (Open)	**−2.34**	**−2.39**	−2.09	**2.56**	**2.97**	**2.96**	−1.46	−1.59	−1.32
Bark (Debarked)	**6.96**	**5.29**	**3.96**	**−6.51**	**−6.59**	**−6.49**	2.12	**6.13**	**7.26**
Soil (Uplifted)	−0.34	1.18	1.45	**−7.65**	**−7.79**	**−7.46**	**−2.96**	−0.37	1.21
Nitrogen	−1.39	0.03	0.68	0.33	0.86	0.84	1.99	2.19	1.88
Carbon	−0.95	−1.29	−1.42	0.44	0.43	0.24	−0.21	−0.89	−1.06
pH	−1.05	−1.50	−1.43	−0.75	−0.92	−1.07	0.65	1.36	1.75
Canopy:Bark	0.73	−0.23	−0.74	**−2.82**	**−2.35**	−2.18	−1.66	−1.51	−1.37
Bark:Soil	−1.85	−1.19	−0.80	**−4.30**	**−4.09**	**−3.59**	**−4.29**	**−3.45**	**−2.83**
Soil:Canopy	0.40	−0.04	−0.28	−1.30	−1.18	−1.38	−1.56	−0.85	−0.33

Note: Bold indicates significant effects after Bonferroni correction for multiple testing.

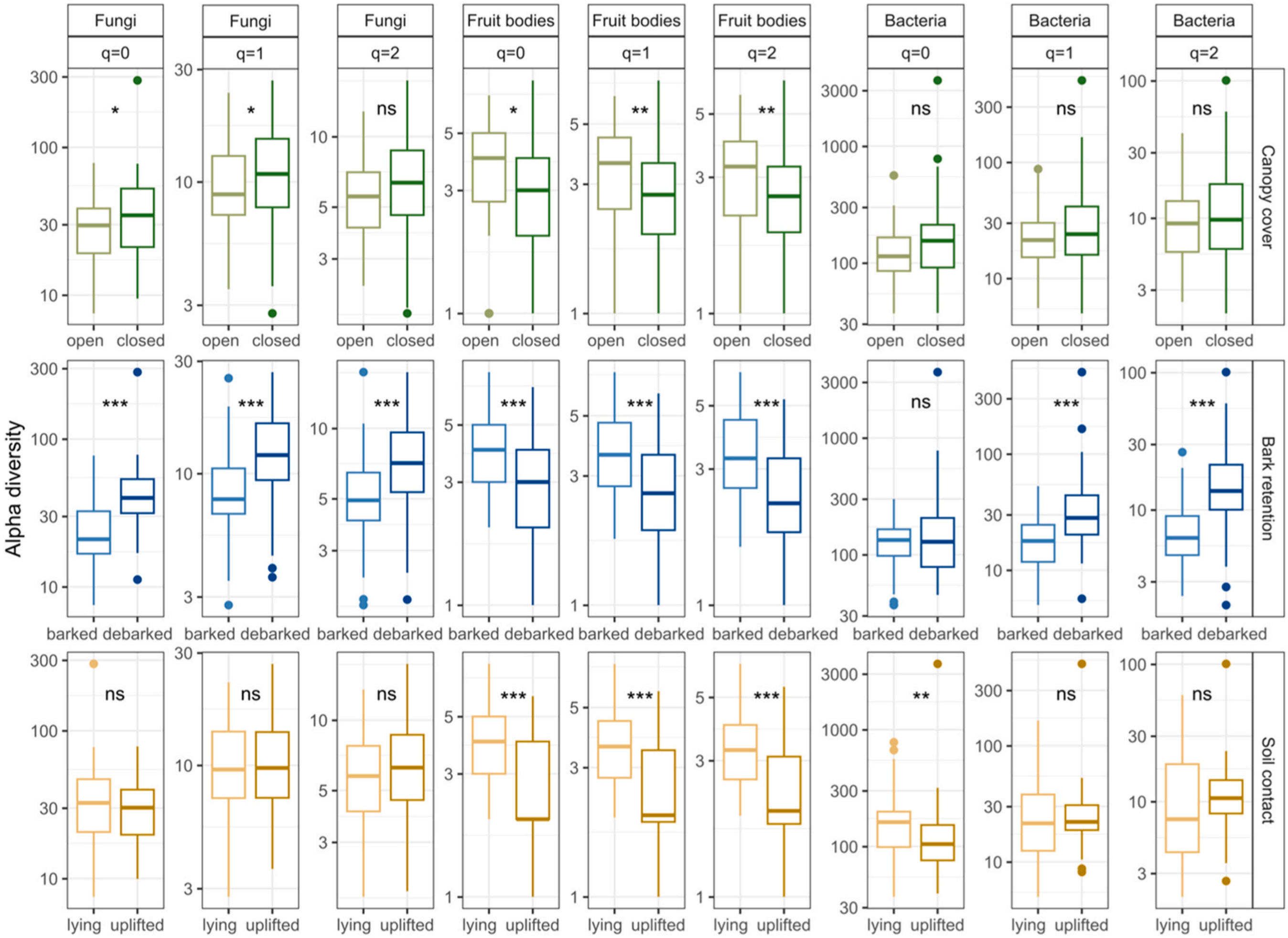

Fig. 2. Effects of treatments on alpha diversity across rare (q=0), common (q=1), and dominant (q=2) fungal OTUs, fungal fruit bodies, and bacterial OTUs. Based on the model results in Table 1, an indication of significance after Bonferroni correction is provided: $p > 0.025$ (ns), $p < 0.025$ (*), $p < 0.005$ (**), $p < 0.001$ (***).

phyloAlpha and thus resulted in communities that are phylogenetically more similar than those with intact bark. On average, negative effect sizes in debarked objects reflect lower phylogenetic diversity than expected. Bacterial communities showed similar results, but SES values were on average lower, and clustering in debarked objects was stronger than for fungi (Table S13; Fig. 5). For fungi, SES.phyloAlpha was significantly lower in closed than in open canopies (Table S13; Fig. 5). Similar to the debarked treatment, fungal communities in closed canopies showed negative effect sizes, indicating phylogenetic clustering.

Our models based on the standardized effect sizes of the mean pairwise phylogenetic distance among objects (SES.phyloBeta) underpin the importance of bark retention. For fungi, the debarking and closed canopy treatments caused a significant decrease of SES.phyloBeta (Table S14; Fig. 5). Thus, on average, pairwise phylogenetic similarity of the communities within the debarked and closed canopy treatments was smaller than expected. This supports the view that these treatments cause very reduced (SES.phyloAlpha) and similar (SES.phyloBeta) phylogenetic lineages. These results together indicate that debarking causes a loss of phylogenetic lineages (Table S15; Fig. 5).

Table 2
PERMANOVA results for molecular distance matrices across Hill numbers, with explanatory variables including treatments, covariates, and treatment interactions.

		Fungi			Bacteria		
		R^2	F	p	R^2	F	p
q= 0	**Canopy**	0.04	5.54	**0.001**	0.03	4.80	**0.001**
	Bark	0.18	27.57	**0.001**	0.14	21.66	**0.001**
	Soil	0.04	5.72	**0.001**	0.06	9.38	**0.001**
	Nitrogen	0.01	1.35	0.202	0.01	1.80	0.028
	Carbon	0.01	2.02	0.503	0.01	1.28	0.493
	pH	0.01	1.37	0.120	0.01	2.06	0.045
	Canopy: Bark	0.01	2.38	**0.019**	0.01	2.44	**0.008**
	Bark: Soil	0.04	7.46	**0.001**	0.05	8.80	**0.001**
	Canopy: Soil	0.01	1.46	0.127	0.01	1.08	0.399
	Residual	**0.65**			**0.66**		
q= 1	**Canopy**	0.03	4.09	**0.001**	0.02	5.14	**0.001**
	Bark	0.16	25.10	**0.001**	0.27	58.20	**0.001**
	Soil	0.06	9.56	**0.001**	0.13	28.57	**0.001**
	Nitrogen	0.01	1.20	0.222	0.02	3.26	**0.008**
	Carbon	0.01	1.47	0.743	0.00	0.13	0.996
	pH	0.01	1.37	0.134	0.02	4.03	**0.008**
	Canopy: Bark	0.01	2.09	0.052	0.01	1.58	0.181
	Bark: Soil	0.09	15.74	**0.001**	0.03	7.59	**0.001**
	Canopy: Soil	0.01	1.56	0.129	0.01	1.13	0.358
	Residual	**0.62**			**0.49**		
q= 2	**Canopy**	0.02	2.51	**0.001**	0.01	2.11	**0.001**
	Bark	0.11	16.19	**0.001**	0.29	63.85	**0.001**
	Soil	0.05	7.48	**0.001**	0.15	33.37	**0.001**
	Nitrogen	0.00	0.70	0.617	0.01	2.59	0.065
	Carbon	0.01	1.09	0.817	0.00	0.19	0.943
	pH	0.01	1.03	0.285	0.01	2.56	0.049
	Canopy: Bark	0.01	1.74	0.071	0.01	1.58	0.221
	Bark: Soil	0.09	14.00	**0.001**	0.04	8.32	**0.002**
	Canopy: Soil	0.01	1.23	0.249	0.00	0.81	0.513
	Residual	**0.69**			**0.47**		

Note: Bold indicates significant effects after Bonferroni correction for multiple testing.

4. Discussion

Simulating different deadwood characteristics after disturbance events, we found that object-scale factors are more important than stand-scale canopy for microbial diversity, supporting H1. Debarked logs showed an increase in molecular fungal and bacterial species diversity, and responses were similar under open and closed canopies, which contrasts with H2. In contrast, fungal fruit body diversity increased with bark retention and soil contact, supporting H2. However, an increase in fruit diversity was related to open canopies, in contrast to our expectation. Null model-based phylogenetic analysis suggests that the object treatments selectively alter assemblages. Notably, debarking selected a reduced set of species-rich phylogenetic lineages (i.e., clustering). Diversity patterns and selective assembly processes likely result from differences in moisture conditions within the dead wood logs between treatments.

4.1. Stand-scale canopy effects

In accordance with our first hypothesis, the effects of the canopy were smaller compared to object-scale factors. Thus, we suggest that object-scale factors outcompete the effects of the abiotic microclimate environment in explaining microbial diversity. This is in line with numerous studies from wood-inhabiting fungi for both metabarcoding and fruit body data and across climate scales (macro- and microclimate) (e.g., Englmeier et al., 2023; Krah et al., 2018). Notably, most studies in this field included host tree species identity as an object-scale factor. The outstanding role of the host tree identity for wood-inhabiting fungal diversity has been attributed to the long-standing co-evolutionary relationships of fungi with their hosts (Baber et al., 2016; Krah, Bässler, et al., 2018; Rieker et al., 2022). In our study, we focused on one host tree species but instead expanded the object scale to include a considerable range of different characteristics reflecting the wide diversity of conditions in managed forests. As with host tree species, our models showed that the effects of deadwood types within one host tree on fungal diversity were greater than those of the canopy cover. This also applies to bacteria, for which the effects of canopy cover on diversity are less pronounced than they are for fungi. Deadwood-inhabiting bacteria have generally received less attention than fungi. However, the few existing local studies support that canopy cover is of minor importance for bacterial alpha and beta diversity (Hagge et al., 2024; Martinović et al., 2022; Müller et al., 2020; Tláskal et al., 2025). Further, at larger spatial scales (across landscapes), variation in temperature, either on the microclimatic or macroclimatic scale, does not seem to govern bacterial diversity in deadwood (Englmeier et al., 2023). From this, we safely assume that stand-scale environmental variability, like microclimate, is less important than object-related factors for overall microbial diversity. Thus, for microbial diversity in deadwood, forest management should focus on object-scale traits such as bark retention or soil contact in addition to the host tree identity. Canopy cover appears less important for microbes, which contrasts with typical recommendations for insects (e.g., Seibold et al., 2016). However, we would like to add one cautionary note. Most studies used coarse woody debris for the comparison between object-scale versus abiotic environmental factors on diversity patterns, but few existing studies suggested that canopy-mediated microclimate becomes more important for diversity if the dimension of the objects decreases (e.g., fine woody debris) (Bässler et al., 2010; Brabcová et al., 2022). The authors attribute this to the fact that fine wood waste is less well-buffered microclimatically than coarse woody debris (Brabcová et al., 2022). Thus, to shed more light on the relative importance of various object-scale factors versus the abiotic macro- and microclimate environment on saproxylic diversity, more studies are needed considering a broad range of deadwood dimensions (diameter and length).

4.2. Bark retention effects

Across our models, the presence of bark is the most important factor for microbial diversity. Metabarcoding data for fungi and bacteria showed a positive relationship with debarking, while for fruit body diversity, we observed the opposite pattern. Bark retention has been ignored in the majority of deadwood experiments (Dossa et al., 2018; Seibold et al., 2015), however, with a few notable exceptions: In a debarking trial for bark beetle control in spruce stands, the diversity of fungal fruit bodies was lower in debarked logs, suggesting that this pattern could potentially apply to both coniferous and deciduous tree species (Thorn et al., 2016). However, another study, also focusing on debarked spruce logs, found no higher number of wood-inhabiting fungal species based on metabarcoding and, in addition, reported lower bacterial OTU richness in debarked logs (Hagge et al., 2019). One explanation for this inconsistency might be that the study by Hagge et al. (2019) considered bark in their sampling, while we controlled for this effect. Indeed, bark has been shown to harbor a number of fungal species, and fungal succession in bark differs from that in wood. Thus, a higher number of species with bark seems intuitive (Kazartsev et al., 2018). Our findings suggest that bark provides chemical and structural protection and may limit colonization, leading to lower diversity (Dossa et al., 2018). In contrast, debarking may encourage colonization and support species establishment. If fungal species coexist in debarked wood, competition might reduce mycelial size per species. However, a minimum size of mycelium is necessary to produce fruit bodies (Bässler et al., 2021). Thus, small mycelial sizes in debarked wood might explain the negative response of fruit body diversity. However, our data do not allow inferences about overall and species-specific fungal biomass, which must be left to further studies. Regarding forest management implications, it is important to note that our study focuses on the early decay stages of deadwood. At this stage, we cannot predict whether the

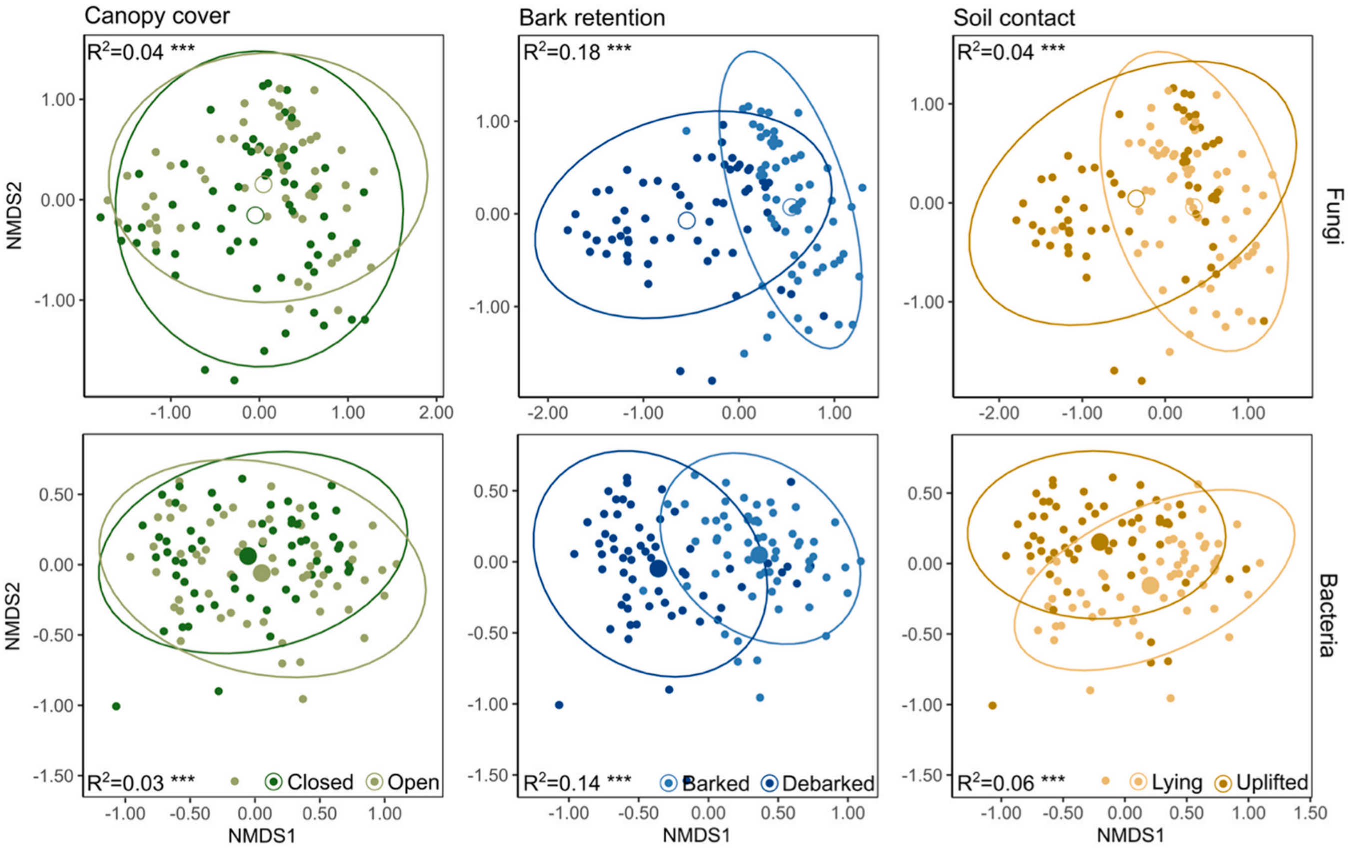

Fig. 3. NMDS plots of fungal and bacterial communities (q=0; k = 2; stress < 0.2). Based on the model results in Table 2, R^2-values and an indication of significance after Bonferroni correction are provided: $p > 0.025$ (ns), $p < 0.025$ (*), $p < 0.005$ (**), $p < 0.001$ (***). Note that this part of the analysis excludes fungal fruit bodies due to data deficiency.

observed molecular diversity, particularly of fungi, will translate into fruit body production and subsequent dispersal. Therefore, management actions should aim to promote a high structural diversity of deadwood, especially when the total amount of deadwood is limited, and be aware that molecular and fruit body diversity may respond differently when assessing the success of such actions.

4.3. Deadwood moisture content effects

Based on the microclimate measurements, we aimed to disentangle the treatment factors, deadwood temperature, and moisture on microbial diversity patterns under open and closed canopy conditions. Note that our temperature data were limited. However, our exploration (Table S2; Fig. S1), as well as previous results (De Frenne et al., 2019; Schreiber, Pouska, et al., 2025), suggested that temperature variability is best explained by canopy cover, justifying our decision to use it as a proxy. We found a negative relationship between fungal and bacterial diversity with moisture based on metabarcoding data, contradicting H3, but the opposite for fungal fruit bodies, supporting H3. This suggests that even under the driest conditions in our setting, a broad range of microbial species can cope physiologically with these conditions. For example, fungi evolved an array of strategies to cope with limited moisture conditions, for example, reduction of osmotic stress (Raffaello et al., 2014) or translocation of water (Boer et al., 2005). As mentioned above, the size and, therefore, the buffer capacity of the substrate seem to be critical factors. We used deadwood 100 cm in length and ca. 25 cm in diameter, which seems sufficient to maintain critical moisture levels for microbes in temperate forests (Pichler et al., 2012; Přívětivý and Šamonil, 2021). However, more studies are needed focusing on the buffer capacity of the deadwood on microbial diversity depending on size, as outlined above, and physical properties among host tree species across succession. Bacterial richness (q = 0) was less responsive to increasing moisture, potentially because bacteria require fewer resources, allowing many rare taxa to persist even when a few taxa become dominant (Jaeger et al., 2023).

The highest fruit body diversity was observed on barked objects with soil contact, reflecting the highest moisture content. We suspect that a minimum mycelial size, together with a critical moisture level, is a precondition for fungal fruiting (Boddy et al., 2014). However, the moisture needed to successfully produce a fruit body varies among species and might depend on species-specific adaptations (Lilleskov et al., 2009). For example, fruit body toughness has been suggested as an adaptation to reduce water loss, while soft-fleshed species are prone to desiccation (Krah et al., 2022). Thus, the positive relationship between fruit body diversity and moisture might be explained by the fact that under benign conditions, a broader range of species can coexist. Conversely, the higher fruit body diversity on barked logs under open canopies might reflect an interplay of factors: while sufficient moisture is a basic precondition for fruiting, additional fruiting cues such as temperature drops, which are more pronounced in open canopies, could further stimulate fruit body formation (Krah et al., 2023; Straatsma et al., 2001). Note that fruit body formation and sexual reproduction are critical to maintaining vital populations for many fungal groups (Ovaskainen et al., 2013). Thus, changing deadwood moisture conditions caused by forest management/climate change interactions could severely affect fungal sexual reproductive behavior and, hence, population vitality.

4.4. Assembly processes

Our analysis revealed that among all treatments, bark retention most strongly affected the standardized effect sizes of the mean pairwise

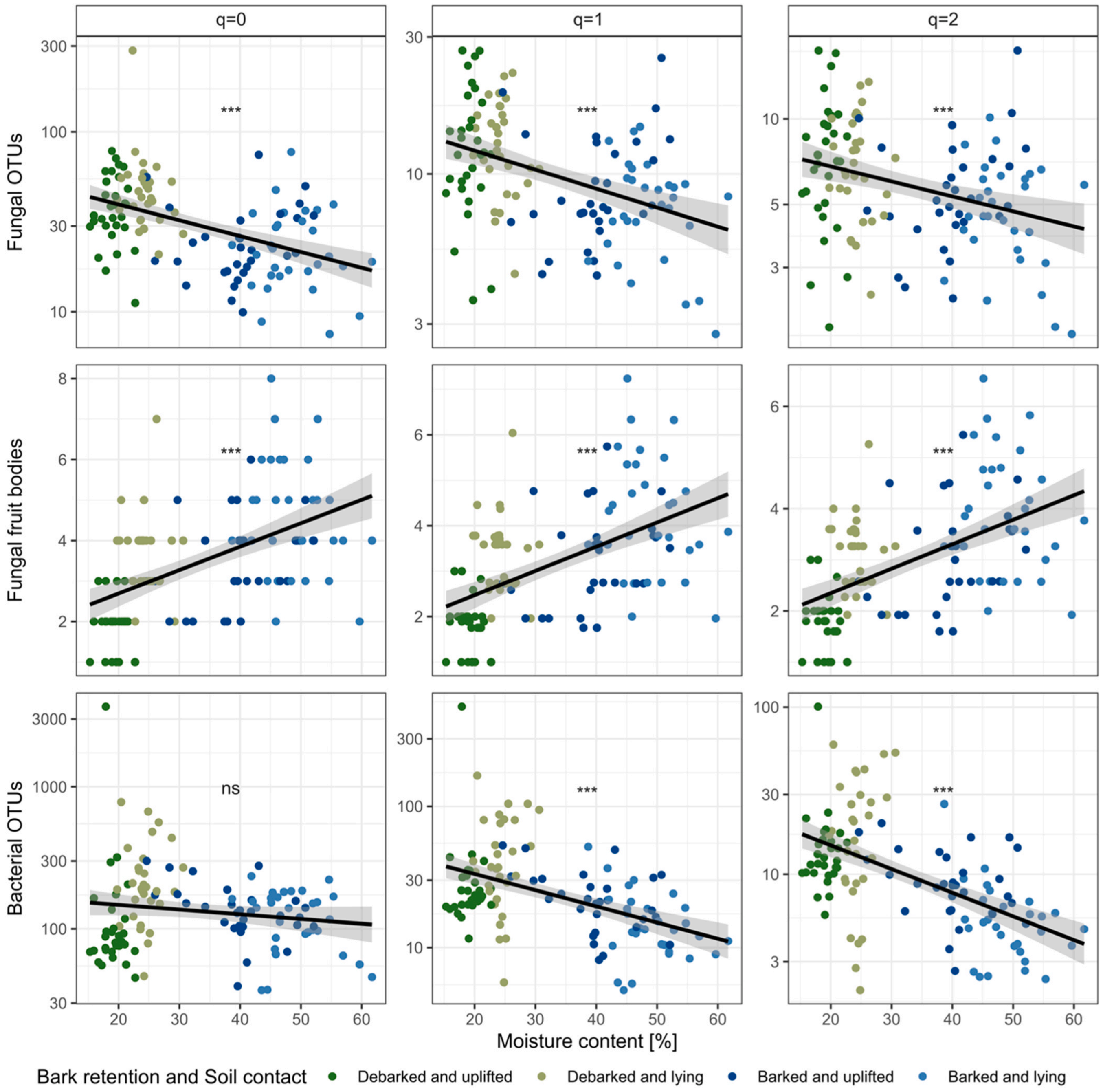

Fig. 4. Alpha diversity across Hill numbers for fungi, bacteria, and fungal fruit bodies versus the mean moisture content of the deadwood objects with a linear trend and confidence interval. Based on the model results in Table S7, an indication of significance after Bonferroni correction is provided: $p > 0.025$ (ns.), $p < 0.025$ (*), $p < 0.005$ (**), $p < 0.001$ (***).

phylogenetic distance within (SES.phyloAlpha) and among (SES.phyloBeta) communities. Debarking significantly reduced SES.phyloAlpha in both fungi and bacteria, with average effect sizes clearly negative (bacteria < -3; fungi ≈ -2), indicating strong phylogenetic clustering. Thus, phylogenetic diversity within debarked objects is smaller than expected and thus indicates selective assembly processes. Further, we found that the SES.phyloBeta values within the debarked objects (mean of all pairwise comparisons within debarked objects) were significantly lower than those based on all pairwise comparisons between barked-debarked and barked-barked objects. This demonstrates that lineages associated with debarked objects are a subset of those occurring on barked objects, reflecting a reduced and more phylogenetically clustered set across objects. Together, these results indicate that debarking caused a selective loss of phylogenetic lineages, supporting H4, and promoted the assembly of similar lineages under treatments representing stressful conditions, supporting H5. Studies focusing on assembly processes of microbial communities in deadwood are scarce. However, in one study, it has been shown that debarking had an influence on microbial assembly processes (Hagge et al., 2019). Debarking increased the proportion of deterministic assembly processes. However, differences in assembly processes among treatments and whether habitat filtering or limiting similarity prevail were not tested (Hagge et al., 2019). As hypothesized, our data support the view that debarking is related to environmental stress for microbial communities caused by limited moisture availability (Fig. S2). Our study thus supports numerous studies from various taxonomic groups and environmental contexts

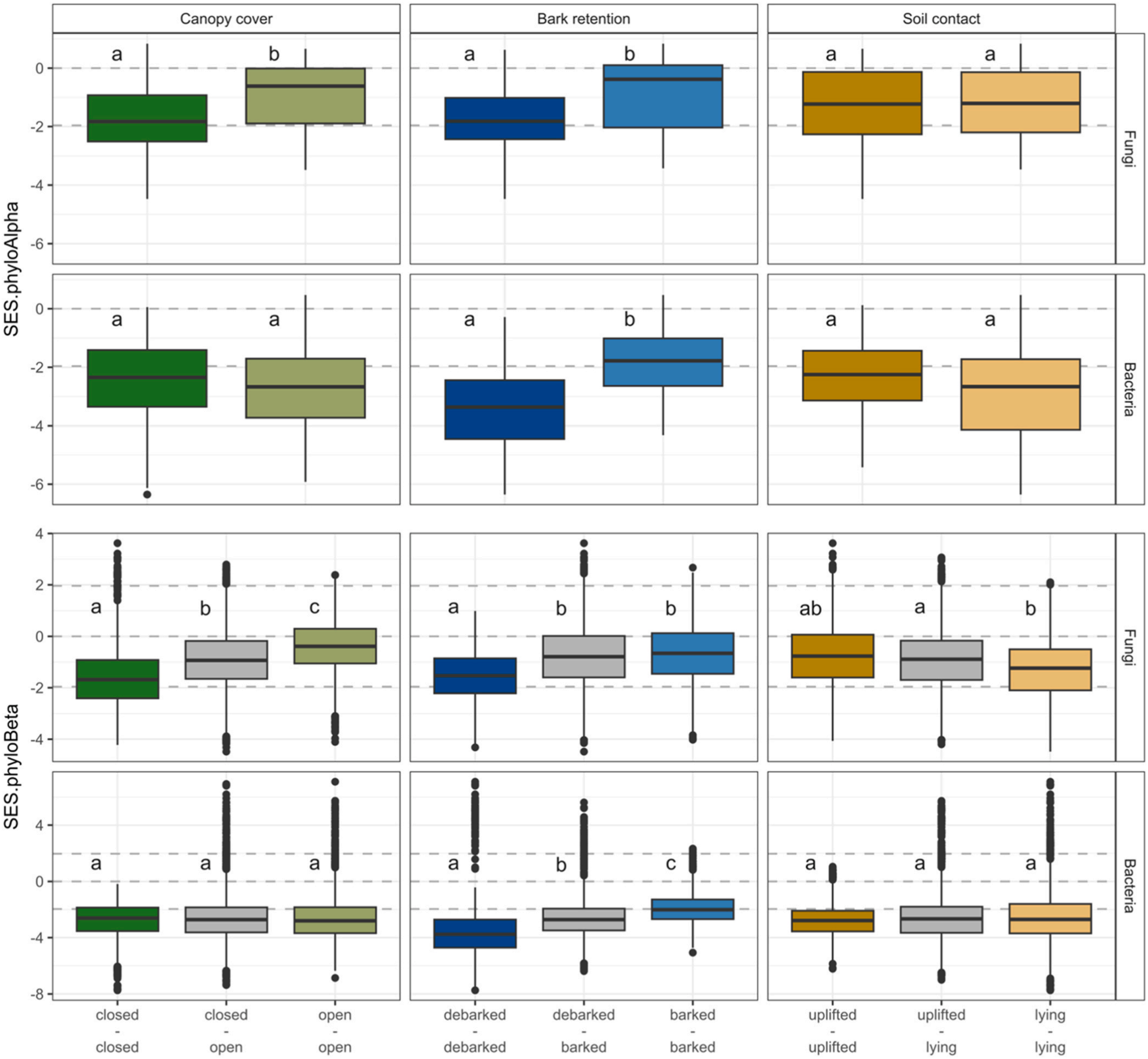

Fig. 5. Phylogenetic community structure of fungi and bacteria across experimental treatments. Standardized effect sizes of alpha (SES.phyloAlpha) and beta diversity (SES.phyloBeta) were calculated using null models, respectively. Negative values indicate phylogenetic clustering, positive values indicate overdispersion. Boxplots show distributions of standardized effect sizes for each treatment, dashed horizontal line indicates the null expectation. Letters above boxplots indicate significant pairwise differences among treatment levels within each factor (from linear mixed-effects models and *post hoc* tests ($p < 0.05$); Tables S13-S15). Levels sharing the same letter are not significantly different.

demonstrating that environmental constraints cause phylogenetic clustering (e.g., Patrick and Stevens, 2016). For example, in one study, it has been shown that avian communities are phylogenetically clustered in less-vegetated habitats considered as unfavorable habitats (Gianuca et al., 2014). In another study, it has been revealed that marine bacterial communities were phylogenetically clustered and suggested that this is due to salinity- and dissolved organic carbon stress (Pontarp et al., 2013). Many conceptual and empirical studies demonstrated that increasing environmental stress acts as a filter selecting for species with certain traits from specific lineages that can cope with unfavorable conditions and thereby reducing the number of coexisting species (e.g., Goberna et al., 2014; Macarthur and Levins, 1967; Sandel, 2018; Sandel et al., 2016; Sommer et al., 2014). The rationale is that only a subset of a species from a pool can coexist that are adapted to the environmental constraints (Weiher et al., 1998). Interestingly, our data showed that filtering towards specific and a reduced set of phylogenetic lineages in debarked stressful environments, species richness increased in both taxa. This means that in debarked objects, more species from the remaining lineages were able to assemble. This might indicate that more species from the remaining lineages could assemble, suggesting the assembly of niche-complementary species that are otherwise not assembled due to weak competitive abilities. This would be consistent with the dominance-tolerance trade-off hypothesis (Maynard et al., 2019). However, to tackle this question, we would need the assembly-relevant functional traits distribution of the species in our setting. Given that we observed thousands of putative microbial species (OTUs), we consider this a great challenge for future studies. Debarking appears to have imposed strong selective pressures on microbial communities, favoring lineages adapted to stressful conditions. Such environmental filtering likely drives phylogenetic clustering, while the coexistence of multiple species under these constraints may be maintained through complementary functional traits.

5. Conclusion

We showed that microbial diversity in deadwood is primarily determined by object-level factors and not by canopy cover at the stand-level. We conclude that object characteristics that determine moisture conditions, like bark retention, are important for alpha and beta diversity. Molecular microbial diversity within wood is higher under more stressful dry conditions. Thus, variations in bark cover caused by natural processes or forest management techniques strongly influence microbial diversity via selective assembly processes. We advise forest managers and conservationists to shift their focus from the stand-level to the characteristics of deadwood objects. Here, however, deadwood enrichment should consider deadwood characteristics that vary greatly in moisture content. While stressful dry conditions boost microbial alpha diversity, benign moisture conditions maintain more phylogenetic lineages and fruit body diversity and thus, most probably functional integrity. We note, however, that canopy cover in our study was used as a proxy for microclimatic conditions, and while our limited data support this approach, continuous microclimate measurements could provide more precise insights into temperature and moisture effects. Furthermore, to complement our picture, we recommend using an RNA-based method to measure the active microbial communities over the complete course of succession using different deadwood dimensions and host tree species in future studies. Finally, linking deadwood characteristics with assembly processes based on both phylogenetic and functional diversity, as well as the related ecosystem processes like decomposition, in future studies would provide further insights about the ecological consequences of forest management decisions.

CRediT authorship contribution statement

Henrik Oechler: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis. **Franz-Sebastian Krah:** Writing – review & editing, Formal analysis. **Jasper Schreiber:** Writing – review & editing, Investigation. **Petr Baldrian:** Writing – review & editing, Investigation, Funding acquisition. **Vendula Brabcová:** Writing – review & editing, Investigation, Funding acquisition. **Harald Kellner:** Writing – review & editing, Investigation, Funding acquisition. **Friederike Roy:** Writing – review & editing, Investigation. **Claus Bässler:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Jasper Schreiber reports financial support was provided by Deutsche Forschungsgemeinschaft. Peter Baldrian reports financial support was provided by Czech Science Foundation. Peter Baldrian reports financial support was provided by Ministry of Education Youth and Sports of the Czech Republic. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.123268.

Data availability

The scession numbers PRJNA1232019 (ITS) and PRJNA1232009 (16S).

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