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Title: Decaying logs and gap positions jointly mediate the structure and function of soil bacterial community in the forest ecosystem

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Abstract

Soil bacteria play a vital role in soil processes within forest ecosystems, yet the changes in the structure and function of soil bacterial community with decaying logs and forest gaps remains inadequately understood. To address this knowledge gap, we conducted an experiment involving the incubation of five decay classes (I–V, at increasing levels of decay) of Minjiang fir (*Abies faxoniana*) logs at forest gap center, gap edge and closed canopy in a subalpine forest on the eastern Tibetan Plateau, China. We employed high-throughput sequencing (Illumina Novaseq) and Functional Annotation of Prokaryotic Taxa (FAPROTAX) to analyze the diversity, composition and function of soil bacterial communities beneath decaying logs. A total of 11,291 operational taxonomic units was observed. After six years, soil bacterial diversity, composition and function exhibited significant variations across log decay classes and gap positions. Soil bacterial alpha diversity beneath decaying logs was significantly higher and lower in decay classes III/IV and I, respectively, and significantly higher under the center/edge of forest gaps than closed canopy. Additionally, Proteobacteria, Acidobacteria, and Actinobacteria were the dominant bacterial phyla, regardless of decay classes and gap positions. The relative abundance of most soil bacterial genera varied significantly with decay classes and gap positions. Results from FAPROTAX analysis showed that chemoheterotrophy and aerobic chemoheterotrophy were dominated functional groups across all samples. Moreover, functional groups associated with soil carbon cycle showed higher abundance beneath highly decayed logs (IV-V), and functional bacteria participating in the nitrogen and sulfur cycles were enriched in the gap center, underscoring the importance of decaying logs and forest gaps

in the succession of soil bacterial communities. Overall, the structure and function of soil bacterial communities showed significant variation depending on the log decay stage, e.g., decay class, with these dynamics being strongly influenced by forest gap positions. Thus, maintaining woody debris in the middle (III) to late (IV) stage of decay in the forest floor, particularly in the center of forest gaps, is beneficial for sustaining soil bacterial biodiversity in forest ecosystems. These results provide insights into managing woody debris for a sustainable forest practice.

Keywords: coarse woody debris, decay classes, soil bacterial diversity, community composition, functional group, forest gap, FAPROTAX

1. Introduction

Soil microorganisms, from a significant functional group within soils, actively engage in critical processes such as organic matter decomposition, mineral weathering, and nutrient cycling, thereby playing key roles in biogeochemical cycles (Lladó et al., 2017; Schimel, 1995). Factors such as soil organic matter concentration (Stokland et al., 2012), soil temperature (Singh et al., 2014), soil moisture (Brockett et al., 2012), and soil pH (Lauber et al., 2009) are considered predominant in mediating the structure and function of soil microbial communities. Although the carbon and nutrients released from decaying logs, and micro-environments such as temperature and humidity created by canopy gaps and logs might exert crucial roles in maintaining the structure and function of soil bacterial community, more studies have highlighted the importance of deadwood for conserving invertebrates and fungi (Andringa et al., 2019; Bani et al., 2018), the effect of decaying logs and forest gap on soil bacterial

communities has rarely been investigated.

The decomposition of logs is a complex ecological process, that exerts crucial roles in the global carbon cycle, soil development, and biodiversity conservation (Ganjegunte et al., 2004; Forrester et al., 2012; Harmon et al., 1986). On one hand, the conditions beneath decaying wood, including temperature and moisture are more stable (Zalamea et al., 2016), creating a favorable environment for the propagation of soil bacteria and other microbes. On the other hand, carbon released from deadwood serves as an essential nutrient source for soil bacteria and other microbes (Stokland et al., 2012), influencing the sequential progression of microbial succession (Eriksson et al., 1990). This suggests that woody debris might directly and indirectly influence soil bacterial communities. Previous studies have observed that the decomposition of logs directly affects the physical, chemical and biological properties of soils beneath the logs (Zalamea et al., 2016). For example, Wojciech et al., (2019a) have found that the stage of decomposition has an impact on the C: N: P stoichiometry of the soil. Soil organic matter under decaying wood increases with the decay stage (Zalamea et al., 2007), and the increase in soil organic matter due to deadwood can stimulate soil aggregate formation, improve soil porosity, and enhance soil enzyme activity (Wojciech et al., 2019b; Wojciech et al., 2019c). Additionally, Minnich et al., (2021) have reported increased microbial activity and biomass in underlying forest soils with deadwood decomposition. Wang et al., (2022a) have observed that the effect of decaying logs on soil fungal diversity varied with decay classes. Wang et al. (2023) further observed that coarse woody debris with decay levels across different succession stages harbor some unique soil bacterial phyla and genera. Despite these findings, the relationship between

78 the structure and function of soil bacterial communities and the presence or not of logs and
79 their decomposition remains underexplored.

80 Forest gaps lead to the redistribution of the canopy and changes in solar radiation and
81 precipitation, resulting in more heterogeneous microhabitats both within and outside of the
82 gaps (Gray et al., 2002; Wu et al., 2018). This alteration affects the dynamics of temperature
83 and moisture on the forest floor, which might directly influence the structure and function of
84 soil bacterial communities. Previous study has found that bacterial growth rates had optimum
85 temperatures around 25-30 ℃, while at higher temperatures lower values (Pietikäinen et al.,
86 2005). In addition, soil moisture is the major factor influencing microbial community structure
87 and enzyme activities (Brockett et al., 2012), and they found that forest floors from the hot and
88 dry forests were associated with enzymes characteristic of water-stress. Furthermore, the
89 micro-environments created by canopy gaps affect the decomposition of logs, thus might
90 indirectly affect soil microbial communities beneath logs. Wang et al., (2022b) have found that
91 forest canopy density significantly alters the nutrient concentrations in decaying logs. Forest
92 gaps have strong effects on C: N: P stoichiometry in highly decayed logs (Wang et al., 2021),
93 and accelerate the degradation of cellulose and lignin during the decomposition of logs (Wang
94 et al., 2022c). Therefore, the gap center with higher surface temperatures and the closed canopy
95 with higher humidity conditions may be beneficial for the growth of different soil microbial
96 communities. To date, the effects of coarse woody debris on microbial communities (Prewitt
97 et al., 2014; Qi et al., 2023), and the effects of forest gaps on litter decomposition (Ni et al.,
98 2015), have been well-documented, but the effect of gap positions on soil bacterial

communitiesbeneath decaying logs remains unknown.

To address this knowledge gap, we conducted an in-situ log incubation experiment in an over-mature Minjiang fir (*Abies faxoniana*) at forest gap center, gap edge and closed canopy on the eastern TibetanPlateau, China. Log decomposition typically takes several decades to complete, making it challenging to study the development of soil microbial communities beneath decaying logs through full decomposition experiments. To address this, we investigate decomposition by dividing fallen logs into five decay classes (I–V, at increasing levels of decay). After six years of incubation, soil bacterial communities beneath and away from decaying logs in different gap positions were analyzed using high-throughput sequencing, and the Functional Annotation of Prokaryotic Taxa (FAPROTAX) method was employed to predict functional groups of soil bacterial communities based on 16S rRNA sequencing data (Louca et al., 2016). Our study aimed to understand how decaying logs and gap positions affect the diversity, composition, and function of soil bacterial communities. Previous studies have shown that the decomposition of coarse woody debris leads to increased soil water content, organic carbon concentration, and nutrient levels, all of which are closely associated with soil microbial communities. Based on this, we hypothesized that (1) the diversity of soil bacterial communities beneath decaying logs would differ from those away from logs and it would increase with the degree of log decomposition, and highly decayed logs would lead to stronger effects on the composition and function of soil bacterial communities. Additionally, forest gaps increase surface temperature and decrease humidity, resulting in increased soil microbial activity. Consequently, we also hypothesized that (2) forest gaps increase the diversity of soil

bacterial communities beneath decaying logs, and the composition and function of soil bacterial communities would be regulated by forest gap positions. The results could help us better understand the function and significance of woody debris in soil biodiversity conservation, and the adaptability of soil microorganisms to the environment in forest ecosystems, and provide clear insight into the preservation of coarse woody debris and the positive effect of forest gaps, which is a key to sustainable forest management in subalpine forests.

2. Materials and methods

2.1 Site description

We conducted this study at the Long-Term Research Station of Alpine Forest Ecosystems in Li County (31°14′-31°19′N, 102°53′-102°57′E; 2458-4619 m a.s.l.), Sichuan, southwestern China. This region is situated in the transitional area between TibetanPlateau and the Sichuan Basin. The annual mean temperature in this region is approximately 2-4 °C, ranging from 23 ℃ (July) to -18 ℃ (January), and annual precipitation is approximately 850 mm (Chang et al., 2019). Seasonally freeze-thaw cycles occur from early November until April of the following year. The fallen log stock is 53 $Mg \cdot ha^{-1}$ and varies from the gap center to the closed canopy (Xiao et al., 2016). The most dominant tree species at our study site is Minjiang fir (*Abies faxoniana*), and cypress (*Sabina saltuaria*), larch (*Larix mastersiana*), and red birch (*Betula albo-sinensis*) are the other main tree species. The soil is classified as Cambisols, featuring a soil organic layer thickness of about 12 cm. The concentration of soil organic carbon and total nitrogen beneath decaying logs ranges from 125.39 $g \cdot kg^{-1}$ to 191.16 $g \cdot kg^{-1}$ and 5.09 $g \cdot kg^{-1}$ to 6.07 $g \cdot kg^{-1}$, respectively.

2.2 Experimental design

Three permanent plots of 100 m × 100 m were established in the over-mature primary Minjiang fir forest inside the above-mentioned Long-Term Research Station of Alpine Forest Ecosystems in August 2006. Within each plot, an elliptical forest gap (50-150 m^2), gap edge close to the gap and a closed canopy next to the gap edge were chosen for log decomposition. In August 2013, logs of decay classes I-V (I: cambium still fresh and bark is intact; II: cambium starting to decay and bark is mostly intact; III: the shape of the cambium is not complete, and the bark is detached or absent; IV: no bark, and the heartwood is rotten, oval; and V: partial collapsed, difficult to identify the shape) with 35 ± 5 cm in diameter and 120 cm in length were incubated on the forest gap center, gap edge and closed canopy (Chang et al. 2019; Wang et al. 2021). As a result, a set of 45 log decomposition samples (3 gap positions × 5 decay classes × 3 replications in each plot) for a total of 135 log samples in this experiment.

2.3 Sampling

In August 2019, after carefully removing decaying logs, we used an auger (10 cm in length and 5 cm in diameter) to collect soil samples from the topsoil (0-10 cm) beneath decaying logs at different positions within the forest gaps in each plot. Simultaneously, topsoil (0-10 cm) samples from the control (3 m away from the decaying logs, CK) were collected. The samples were carried in a cooler with ice packs to the lab. 162 soil samples in all, comprising 3 plots ×3 gap positions × (1 CK + 5 decay classes) × 3 replicates, were collected. After removing any visible living plant material, soil water content (SWC) was measured using roughly 20 g of soil. Approximately 10 g of air-dried soil samples were used for pH measurement after passing

through a 2 mm sieve, and subsamples were kept at -70 °C for molecular analysis and 4 °C for biochemical analysis, respectively. Molecular biochemical analysis was conducted on three replicate samples mixed, resulting in a total of 54 samples.

2.4 Soil physical, chemical and biological analysis

Soil water content was calculated by weighing the samples both before and after drying. A pH meter was used to measure the pH of the soil at a ratio of 1:2.5 (m/v) soil to water. The concentrations of soil organic carbon (C), total nitrogen (N), and total phosphorus (P) were measured using potassium dichromate oxidation-ferrous sulfate titrimetry, Kjeldahl nitrogen determination, and molybdenum-antimonycolorimetry, respectively (Lu, 1999). Chloroform fumigation and K_2SO_4 extraction were used to determine the amount of soil microbial biomass carbon (MBC) and microbial biomass nitrogen (MBN) (Brookes et al., 1985; Vance et al., 1987). Chloroform fumigation and $NaHCO_3$ extraction were used to measure the amount of soil microbial biomass phosphorus (MBP) (Brookes et al., 1982).

2.5 DNA extraction, PCR amplification and high-throughput sequencing

Using the FastDNA Spin Kit for Soil (MP Biomedicals, Solon, USA) following the manufacturer's instructions, microbial DNA was extracted from the samples. Agarose gel electrophoresis and ultraviolet absorbance (ND1000, Nanodrop, Thermo Fisher Scientific, Waltham Mass, USA) were used to assess the purity of the DNA. Dilute DNA o 1 ng/μl with sterile water and then kept -20 °C until analysis.

At Novogene Genomics Institute (Beijing, China), the 16S gene's V3-V4 hypervariable

region was amplified, purified, quantified, pooled, and sequenced on an Illumina NovaSeq platform. The primer pair 341F (CCTAYGGGRBGCASCAG)/ 806R (GGACTACNNGGGTATCTAAT) was used for amplification. Every sample was amplified three times, and at no stage were template controls used. Three repeated PCR amplicons were pooled and detected by electrophoresis in a 2% (w/v) agarose gel, and purified with a GeneJET Gel Extraction Kit (Thermo Fisher Scientific, Waltham Mass, USA). Pair-End 250 was used for sequencing on the Illumina NovaSeq platform. To extract raw tags, barcode sequences were spliced using FLASH (v 1.2.7) software (Zhang et al., 2014). Using Quantitative Insights Into Microbial Ecology (QIIME) (v1.9.0) software, clean tags were created by quality filtering the raw tags (Bokulich et al., 2013; Caporaso et al., 2010). The UCHIME algorithm was used to eliminate chimera sequences (Edgar et al., 2011). At a 97% similarity threshold, the remaining sequences were grouped to generate operational taxonomic units (OTUs) (Edgar, 2013). Mothur software and the SILVA132 SSUrRNA database were used to analyze bacterial species annotation (Edgar, 2013; Wang et al., 2007). MUSCLE software was used to quickly align numerous sequences to determine the phylogenetic relationships of all OTUs that represent sequences (Edgar, 2004). The least amount of data from each sample was used to do normalization, and the normalized data served as the foundation for all subsequent analyses.

A range of statistical analysis indexes in alpha diversity analysis to estimate species diversity (Shannon and Simpson indices) and richness (Chao1 and ACE indices). Additionally, FAPROTAX was used to further analyze the bacterial functional groups (Louca et al., 2016). The dataset acquired by FAPROTAX was compared with the bacterial OTUs, and the default

203 settings were applied to the output functional table.

204 **2.6 Statistical analyses**

205 The chi-squared test was used to check the normality of all variables (soil physicochemical
206 properties, alpha diversity indices, bacterial taxa composition, and proportion of functional
207 groups). Tukey's honestly significant difference (HSD) test was used to examine the differences
208 in soil bacterial alpha diversity among log decay classes and gap positions when the results of
209 variance analysis conducted with general linear models were significant at P =0.05. The HSD
210 test and the Wilcoxon rank-sum test were used to assess the effects of decay classes and gap
211 positions on the relative abundance of soil bacteria at the phylum and genus levels, respectively.
212 Permutational multivariate analysis of variance (PERMANOVA) based on Bray-Curtis
213 distance and analysis of similarity (ANOSIM) were used to test the effects of log decay classes
214 and gap positions on soil bacterial communities, respectively. The results were visualized using
215 two-dimensional Non-metric multidimensional scaling (NMDS) analysis based on the Bray-
216 Curtis distance. The linear discriminant analysis (LDA) effect size (LEfSe) method was used
217 to select the differences in soil bacterial taxa (Segata et al., 2011). LDA> 4 and $P < 0.05$ were
218 the significance standards for decay classes and gap positions at the taxonomic level.

219 Heatmaps and cluster analysis were used to exhibit the distribution and classification of
220 bacterial functional groups among decay classes and gap positions, while the Kruskal–Wallis
221 test was used to distinguish functional groups that were significantly different between groups.
222 Principal component analysis (PCA) was used to visualize the functional group structure
223 among decay classes and gap positions. Relationships between bacterial diversity, the relative

abundances of dominant phyla and genera, and the physicochemical characteristics of the soil were explored using redundancy analysis (RDA). The HSD, Wilcoxon rank-sum, and Kruskal–Wallis tests were conducted utilizing SPSS 20.0 (IBM Corporation, Armonk, USA). The VEGAN package in R was used for additional statistical analyses (Oksanen et al., 2013; R Development Core Team, 2015). At $P < 0.05$, the statistical tests were deemed significant.

3. Results

3.1 Diversity and taxa composition of soil bacterial community

After controlling for raw sequence quality, a total of 4,792,778 raw bacterial sequences and 3,443,963 high-quality bacterial sequences were retained across 54 soil samples beneath decaying logs. At a cutoff sequence similarity of 97%, the sequence data were classified into 11,291 bacterial OTUs. Soil bacterial communities beneath decaying logs exhibited a higher number of independent OTUs in comparison to CK (Fig. S1a), with the highest observed for decay classes I (Fig. S1b). Additionally, the independent OTUs of soil bacterial communities beneath decaying logs were most pronounced for the gap center (Fig. S1c). The alpha diversity indices of soil bacterial communities showed substantial differences among log decay classes, and most samples also exhibited significant variations among gap positions ($P < 0.05$) (Fig. 1). Soil bacterial alpha diversity beneath decaying logs was significantly higher and lower in decay classes III/IV and I, respectively, and significantly higher under the center/edge of forest gaps than closed canopy.

Three of the most common bacterial phyla were Proteobacteria (33.0-57.1%), Acidobacteria (21.7-50.3%), and Actinobacteria (5.9-10.2%), with over 74% of the total reads

(Fig. 2a). During the process of log decomposition, the relative abundance of Proteobacteria in soils beneath decaying logs increased first and then decreased in the gap center and gap edge, but gradually decreased in the closed canopy (Fig. 2a and Fig. S2a-c). Compared to decay class I, the relative abundance of Acidobacteria in soils for decay classes IV and V was significantly higher, while that of Actinobacteria varied slightly with decay classes ($P > 0.05$). In addition, log decay classes had a considerable effect on the relative abundances of most phyla (Fig. S2a-c). Throughout all samples, *Candidatus Solibacter* (2.1-4.9%), *Bryobacter* (1.5-5.1%), *Bradyrhizobium* (1.0-5.8%), *Acidibacter* (1.0-3.7%) were four of the most abundant genera (Fig. 2b). The relative abundance of *Bryobacter* and *Bradyrhizobium* in soils beneath highly decayed logs was higher (Fig. 2b and Fig. S2d-f).

The relative abundance of Proteobacteria was highest in the gap edge, and that of Acidobacteria in soils was higher in the closed canopy than in the gap edge, while that of Actinobacteria was lower in the closed canopy than in the gap edge (Fig. 2 and Fig. S3). The taxa composition of soil bacterial communities in the gap edge was similar to that in the closed canopy (Fig. 3a). The taxa composition of soil bacterial communities varied significantly with log decay classes and gap positions (stress <0.2) (Fig. 3b-c). Additionally, the PERMANOVA test and ANOSIM analysis further confirmed that there were significant differences in soil bacterial communities between decay classes CK/I/II and IV/V, as well as between pairwise classes III-V (Table S1) and all gap positions (Table S2). Besides, compared to CK and other classes, soil characteristic bacteria beneath the logs for decay class I included Holophagae, Burkholderiaceae and Gammaproteobacteria, those for decay class II included

Nitrosomonadaceae, Chthoniobacterales and Verrucomicrobiae (Fig. 3d-e). More importantly, those for decay class V included Clostridia (Firmicutes) and Acidobacteria. Moreover, soil characteristic bacteria in the closed canopy included Alphaproteobacteria and Acidobacteria (Fig. 3f-g), those in the gap edge included Rhizobiales (Proteobacteria), and those in the gap center included Deltaproteobacteria.

3.2 Functional groups of soil bacterial community

The most abundant functional groups were chemoheterotrophy and aerobic chemoheterotrophy in soil bacterial communities (Fig. 4a). There were notable variations in the relative abundance of chemoheterotrophy among decay classes, but not among gap positions. Meanwhile, slightly significant differences in the relative abundance of aerobic chemoheterotrophy and other functional groups were also found among decay classes (Fig. 4b) and gap positions (Fig. 4c). More importantly, the higher relative abundances of the methylotrophy and hydrocarbon degradation functions associated with the soil carbon cycle were observed beneath highly decayed logs (IV-V) ($P < 0.05$; Fig. 4b), and the aerobic nitrite oxidation and nitrification functions participating in the nitrogen cycle, and sulfate respiration and respiration of sulfur compounds participating in the sulfur cycle had the highest relative abundances in the gap center ($P < 0.05$; Fig. 4c). Conspicuous segregation of functional group composition of soil bacterial communities was observed between CK and decay classes IV-V (Fig. 4d) and among different gap positions (Fig. 4e).

3.3 Correlations of soil bacterial community with soil physicochemical properties

Soil organic matter, soil water content, and soil pH were important factors correlated with soil bacterial community structure (Fig. 5). The Shannon diversity indices were positively correlated with soil organic carbon, total nitrogen, total phosphorus, microbial biomass and soil water content, and negatively correlated with soil pH. The Chao1 and ACE richness indices were positively correlated with soil temperature. The relative abundance of Acidobacteria was positively correlated with soil organic carbon, total nitrogen, total phosphorus, and C/N/P stoichiometric ratios and microbial biomass, and negatively correlated with soil pH, while the opposite trend was found for Actinobacteria. The relative abundance of *Bryobacter* and *Bradyrhizobium* was positively correlated with soil organic carbon, total nitrogen, total phosphorus, microbial biomass and soil water content, and negatively correlated with soil pH.

4. Discussion

4.1 Changes in diversity and composition of soil bacterial community with log decay classes and gap positions

The number of soil bacterial OTUs beneath decaying logs is higher than soils without logs (Fig. S1). This is because decaying logs serve as an additional source of nutrients and help maintain a consistent soil temperature and moisture (Zalamea et al., 2016), in contrast to soils without logs. This finding suggests that decaying logs could create favorable habitat conditions for certain soil bacterial species, and introduce new species to the soils without logs, potentially involved in wood decomposition. Moreover, the species diversity and richness of soil bacterial

communities initially increase and then decrease during the decomposition process (Fig. 1), which is partially consistent with our first hypothesis. In our study, soil bacterial diversity indices were positively correlated with soil organic carbon, total nitrogen, total phosphorus, C/N ratios, and microbial biomass, and these components gradually increased with log decomposition, indicating that log decomposition released a large amounts of active organic carbon (AOC) and nutrients (Tláskal & Baldrian, 2021), raising soil organic matter content (Zalamea et al., 2007), promoting high survival rates and increasing soil bacterial diversity. However, logs in decay class V, which are fragmented and have less available carbon and more refractory substances, result in more intense competition among species, leading to the decrease in richness. Additionally, soil bacterial alpha diversity was higher under the center/edge of forest gaps than in closed forest canopies (Fig. 1), which is consistent with our second hypothesis. Zhou et al., (2023) have also found that the Gram-positive bacteria, Gram-negative bacteria, and total bacteria were significantly greater in the forest gap center and gap border compared to those in the closed canopy. Soils beneath decaying logs in the center of forest gaps may have more microenvironments, allowing for the co-existence of different species. Furthermore, the presence of abundant nutrients can reduce microbial diversity while favoring the growth of specific groups, leading to an accumulation of microbial biomass (Banerjee et al., 2016). Some studies suggest that soil physicochemical properties and microbial communities are influenced by forest gap size (Muscolo et al., 2007; Schliemann & Bockheim, 2014). Consequently, the effect of decaying logs on soil bacterial diversity might be influenced by abiotic factors such as gap size.

Proteobacteria, Acidobacteria and Actinobacteria dominated the soil bacterial communities regardless of log presence or not, log decay classes and gap positions (Fig. 2). This pattern was in agreement with the soils without logs (Shang et al., 2023). Delgado-Baquerizo et al. (2018) have aslo demonstrated that these three bacterial phyla are the dominant group of global forest soil bacterial communities. Proteobacteria exhibit an enormous diversity in morphology, physiology, and metabology, which are crucial for global carbon, nitrogen, and sulfur cycling (Kersters et al., 2006). The relative abundance of Proteobacteria in soils beneath highly decayed logs was lower, possibly due to the dominance of α-proteobacteria and β-Proteobacteria. α-proteobacteria adapt to low-nutrient conditions (Lladó et al., 2016), while the relative abundances of ß-Proteobacteria are positively correlated with C mineralization rates (Fierer et al., 2007). In brief, a lot of Proteobacteria are copiotrophic, meaning that they become abundant when labile substrates are available (Fierer et al., 2007).

The relative abundance of Acidobacteria in soils beneath highly decayed logs was higher. A vast array of lignocellulose-decomposing and carbohydrate-active enzymes that are involved in the breakdown, utilization, and biosynthesis of various carbohydrates can be produced by Acidobacteria (Lladó et al., 2016), promoting the decomposition of logs. Fierer et al. (2007) have demonstrated that the relative abundance of Acidobacteria is significantly negatively correlated with soil pH value and net carbon mineralization rate. Through interactions among soil elements such as the precipitation of ions, soil pH indirectly influences the structure of microbial communities (Lammel et al., 2018). Ricketts et al. (2018) have also observed that the differences in soil bacterial communities and functions between the presence and none of

ash trees are largely driven by Acidobacteria. The results suggest that decaying logs may affect the structure of soil bacterial communities by changing soil pH. Besides, soil characteristic bacteria beneath the logs for decay class V included *Clostridia* (genera in the phylum Firmicutes), which is anaerobic or microaerobic, and only a few species can grow under aerobic conditions, indicating that it has extremely strong resistance beneath highly decayed logs with less available carbon. In addition, the relative abundance of *Bradyrhizobium* in soils beneath highly decayed logs was higher. It is a species of rhizobium in the alphaproteobacterial that was linked to nitrogen fixation, playing an important role in the soil carbon and nitrogen cycle (Vaninsberghe et al., 2015). Tláskal & Baldrian (2021) have also found that *Bradyrhizobium* is richer in the middle and late decomposition stages of wood, indicating that it has the same trend of changes during wood decomposition in both deadwood and soils beneath them. Therefore, decaying logs could alter the function of soil bacterial communities participating in nitrogen fixation.

The composition of soil bacterial communities varied depending on the position within the forest gaps. For example, the relative abundance of Acidobacteria was the highest in the closed canopy, possibly due to lower soil pH, the major predictor of variation in community network structure across forest soils (Kerfahi et al., 2024), indicating that the canopy created more favorable pH conditions for some soil bacteria like Acidobacteria. Additionally, the relative abundance of Actinobacteria was the lowest in the closed canopy, possibly because Actinobacteria tend to be more active in soils with lower water content (Unger et al., 2009). Furthermore, Rhizobiales were characteristic of soils beneath decaying logs in the gap edge

(Fig. 3), suggesting that the conditions in the gap edge might favor nitrogen-fixing bacteria. While the reasons behind these variations in soil bacteria at the gap edge require further investigation, it is likely that the dominant bacterial phyla play a role in decomposing logs. Changes in soil bacteria composition could also be linked to the heterogeneity of soil organic matter and nutrient levels in different forest gap positions, such as carbon composition, nitrogen availability and total phosphorus (Cederlund et al., 2014; Liu et al., 2018; Scharenbroch & Bockheim, 2007).

4.2 Response of soil bacterial functional groups to log decomposition and gap positions

Different soil bacterial functional groups beneath decaying logs formed at distinct decay classes. Chemoheterotrophy and aerobic chemoheterotrophy had the highest relative abundance across all samples (Fig. 4), consistent with the previous study (Wang et al., 2023). The methanotrophy and hydrocarbon degradation functional groups associated with the soil carbon cycle had a higher abundance beneath highly decayed logs, suggesting that the shift in the microbial community caused by log decomposition may affect the chemical stability of soil organic matter. The increased abundance of aerobic nitrite oxidation and nitrification (participating in the nitrogen cycle), and sulfate respiration and respiration of sulfur compounds (participating in the sulfur cycle) in soils beneath decaying logs in the gap center could be the consequence of the increase of the mineralization and nitrification of soils with the development of understory vegetation (Ritter, 2005), as well as the potential presence of sulfides in penetrating rain and changes in soil pH caused by it (Lyu et al., 2022). Bonkowski (2004) has observed that the organic forms of nitrogen and sulfur can be transferred to more

389 inorganic forms through microbial depolymerization and mineralization. In our study, despite
390 differences in soil bacterial diversity and composition among forest gap positions, few
391 significant differences were detected concerning the most potential functional groups of the
392 soil bacterial communities. These findings may suggest that a high level of functional
393 redundancy exists within the soil bacterial communities considered here (Hollister et al., 2010),
394 while functional redundancy is assumed to be widespread in soil microbial communities
395 (O'Donnell et al., 2005).

396 ## 5 Conclusion

397 The diversity, composition, and function of soil bacterial communities beneath decaying
398 logs are intricately affected by log decomposition and gap positions. These results are
399 consistent with our hypotheses. We found that the soil bacterial community structure beneath
400 decaying logs in the middle stage (III) and late stages (IV) was similar, and different from
401 communities in the early stages (I). Highly decayed logs (IV-V) created favorable water and
402 pH conditions for soil bacterial functional groups associated with the carbon cycle.
403 Simultaneously, soil bacterial communities showed substantial variation based on gap positions.
404 Forest gaps exerted strong regulation on bacterial functional groups participating in nitrogen
405 and sulfur cycles, as well as soil bacterial diversity. Our findings suggest that both decaying
406 logs and forest gaps play a crucial role in shaping the structure and succession of soil bacterial
407 communities in forest ecosystems. Thus, maintaining woody debris in the middle (III) to late
408 (V) stage of decay in the forest floor, particularly in the center of forest gaps, can be beneficial
409 for sustaining soil bacterial biodiversity in forest ecosystems. Future studies on forest soil

biodiversity conservation and restoration should take into account the decomposition stages of woody debris and variations in forest disturbance. These findings could provide valuable insights into managing woody debris for a sustainable forest development.

Author contributions

Qin Wang: Data Curation, Formal analysis, Investigation, Visualization, Writing - Original Draft. Zhuang Wang: Formal analysis, Investigation. Josep Peñuelas: Supervision, Writing - Review & Editing, Funding acquisition. Rui Cao: Formal analysis, Investigation. Lifeng Wang: Formal analysis, Investigation. Wanqin Yang: Conceptualization, Resources, Supervision, Writing - Review & Editing, Funding acquisition. All authors contributed critically to the drafts and gave final approval for publication.

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Conflict of Interest Statement

All authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest or non-financial interest in the subject matter or materials discussed in this manuscript.

Figure captions

Fig. 1 Indices of Shannon (a), Simpson (b), Chao1 (c) and ACE (d) of soil bacterial communities. CK, the treatment away from decaying logs; I-V, decay classes I-V. GC, gap center; GE, gap edge; CC, closed canopy. Different capital letters indicate significant differences ($P < 0.05$) among different decay classes at the same gap position. Different lowercase letters indicate significant differences ($P < 0.05$) among different gap positions at the same decay class.

Fig. 2 Relative abundances of soil bacteria at the phylum (> 0.5%) (a) and genus (> 0.3%) (b) beneath and away from decaying logs (ranked by the sum of means). Groups accounting for <0.5% of phyla and 0.3% of genera are integrated into 'others'. CK, the treatment away from decaying logs; I-V, decay classes I-V. GC, gap center; GE, gap edge; CC, closed canopy. Data are the means of three samples for each group.

Fig. 3 Changes in soil bacterial community beneath decaying logs according to the 16S rRNA. Heatmap of taxonomic composition (a). Non-metric multidimensional scaling (NMDS) analysis in soil bacteria (b-c). LDA scores and Cladogram generated by linear discriminant analysis effect size (LEfSe) for the bacterial taxa among decay classes (d-e) and gap positions (f-g) (LDA>4). CK, the treatment away from decaying logs; I-V, decay classes I-V. GC, gap center; GE, gap edge; CC, closed canopy.

Fig. 4 Variations in functional groups of soil bacteria according to the FAPROTAX database annotation. Relative abundance of the top-10 dominant functional groups (a). Heatmap of the top-35 dominant functional groups (b-c). * $P < 0.05$, ** $P < 0.01$. Kruskal-Wallis test. Principal component analysis (PCA) of bacterial communities (d-e). CK, the treatment away from decaying logs; I-V, decay classes I-V. GC, gap center; GE, gap edge; CC, closed canopy.

Fig. 5 Redundancy analysis (RDA) of Alpha diversity (a), dominant phyla (b) and dominant genera (c) of soil bacteria communities with soil organic carbon (C), total nitrogen (N), total phosphorus (P), C/N/P stoichiometric ratios, microbial biomass carbon (MBC), microbial biomass nitrogen (MBN), microbial biomass phosphorus (MBP), and MBC/MBN, MBC/MBP, MBN/MBP ratios, soil temperature (ST), soil water content (SWC) and pH value (pH).

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